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THE STATUS AND SYSTEMATIC POSITION OF THE SPECIES OF THE BOPYRID ISOPOD GENUS *PHYLLODURUS* STIMPSON, 1857

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Abstract.—Markham, J. C., Bermuda Biological Station for Research, Inc., St. George's West, 1–15, Bermuda.—The monotypic bopyrid isopod genus *Phyllodurus* Stimpson, 1857, is assigned, as type-genus and sole representative, to a new subfamily, Phyllodurinae, intermediate in characters and mode of host selection between the subfamilies Athelginae Codreanu and Codreanu and Ioninae H. Milne Edwards. An annotated synonymy for the single species of *Phyllodurus*, *P. abdominalis* Stimpson, 1857, is presented. The only other nominal species of *Phyllodurus*, *P. robustus* Pearse, 1953, is placed in synonymy with *Pseudione upogebiae* Hay, 1917.

The systematic position of the species *Phyllodurus abdominalis* Stimpson within the family Bopyridae has long been uncertain because it does not fit into any of the currently recognized subfamilies. Moreover, another species, *P. robustus* Pearse, was clearly incorrectly assigned to this genus, but its true identity could not be determined from the published description. To resolve these problems, I am proposing a new subfamily for *Phyllodurus abdominalis* and presenting evidence that *P. robustus* is a junior synonym of *Pseudione upogebiae* Hay, 1917.

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Family BOPYRIDAE Rafinesque, 1815
Subfamily PHYLLODURINAE, new subfamily

Diagnosis.—Female: All segments distinct; body axis nearly straight; frontal lamina, coxal plates and dorsolateral pereonal bosses all moderately developed; no middorsal projections on pereomeres; pleon triangular, markedly narrower than pereon, extending far posteriorly; pleon of 6 pleomeres, first with dorsal papillose process at each side of anterior margin; pleon bearing pedunculate falcate lateral plates and pleopodal exopodites, both with entire margins, on each of first 5 pleomeres, all of nearly same

size; no pleopodal endopodites; terminal pleomere produced into sharp point, bearing uniramous uropods of same structure as lateral plates and exopodites. Male: Body more than twice as long as wide; all body regions and segments distinct; pleon of 6 pleomeres, last 5 produced into constricted lateral lobes extending posterolaterally; 5 pairs of uniramous sac-like pleopods; no uropods; terminal pleomere pointed posteriorly. Abdominal parasite of *Upogebia*.

Type-genus, and sole representative, *Phyllodurus* Stimpson, 1857

Discussion.—Phyllodurus Stimpson has always been difficult to place within the family Bopyridae because it has not fit into any of the established subfamilies. Shiino (1965) placed it in the "*Athelges*-group" (=Athelginae Codreanu and Codreanu), and in an unpublished treatment of the family Bopyridae, I tentatively assigned it to the subfamily Ioninae H. Milne Edwards. Clearly, its affinities are closest to these two subfamilies. It differs from all other athelgines in that their females are always noticeably distorted, their pereomeres are often only obscurely separated, their heads are reduced, deeply embedded in their pereons and often partly fused with some pereomeres; the males of the Athelginae all completely lack pleonal segmentation and appendages; and their hosts, while infested abdominally, are always paguroids. *Phyllodurus* differs from all ionines in that the females of the latter are at least moderately distorted; their pleons are deeply embedded in their pereons; the pleonal appendages are all elongate and with tuberculate or digitate margins; male ionines are relatively more elongate, and their pleomeres are not laterally produced; and the hosts of ionines, although occasionally callianassids and upogebiids (much more often brachyurans), are infested only branchially.

On the basis of morphology and host selection, *Phyllodurus* (and thus its subfamily Phyllodurinae) seems to represent an evolutionary link among several bopyrid subfamilies, as Shiino (1952, 1965) has pointed out. The subfamily Pseudioninae, taken as the most generalized, is largely restricted to anomuran hosts, some species of the rather primitive genus *Pseudione* infesting the genera *Callianassa* and *Upogebia*. The subfamily Ioninae, which shares many morphological characters with Phyllodurinae, contains mostly parasites of brachyurans, but several of the most primitive ionines, including all species of *Ione*, the single species of *Procepon* and one species of *Hypocepon*, infest callianassids. All members of the Pseudioninae and the Ioninae are branchial parasites, in contrast with *Phyllodurus*. The subfamily Phyllodurinae shares many morphological characters and the location of attachment with the Athelginae, but members of these two subfamilies infest hosts in different superfamilies within the infraorder Anomura.

Phyllodurus Stimpson, 1857

Phyllodurus Stimpson, 1857:511 [Type-species, by monotypy, *Phyllodurus abdominalis* Stimpson].

Diagnosis.—As for subfamily Phyllodurinae.
Only one species, *Phyllodurus abdominalis* Stimpson.

Phyllodurus abdominalis Stimpson, 1857

Phyllodurus abdominalis Stimpson, 1857:511–513 [Type-localities, Puget Sound, Washington, and Tamales Bay, California; infesting "the common *Gebia*" (evidently = *Upogebia pugettensis* (Dana)].—Lockington, 1877: 57 [Tomales Bay; infesting *U. pugettensis*; first description of male]; 1878:299–300 [Tomales Bay; infesting *U. pugettensis*].—Stebbing, 1893: 418.—Calman, 1898:261, 282 [Puget Sound; host unspecified].—Richardson, 1899a:868; 1899b:337; 1900:309; 1904a:78 [San Francisco Bay, California; infesting *U. pugettensis*]; 1905:540–544; figs. 582–585.—Bonnier, 1900:171, 215–217, 351.—Holmes, 1900:158.—Gerstacker and Ortmann, 1901:184, 235–236, 266.—Nierstrasz and Brender à Brandis, 1923: 80; 1931:209 [Nanaimo, British Columbia; no host recorded].—Fee, 1926:39 [Departure Bay, British Columbia; infesting *U. pugettensis*].—Fraser, 1932:64 [Nanaimo, British Columbia, and San Juan Islands, Washington; infesting *U. pugettensis*].—MacGinitie, 1935:658, 659–660, 704, 708 [Monterey Bay, California; infesting *U. pugettensis*].—Hatch, 1947:164, 224; pl. IX, figs. 108, 109.—MacGinitie and MacGinitie, 1949: 265, 266, 292; fig. 120c [Tomales Bay; infesting *U. pugettensis*]; 1968: 265, 266, 292; fig. 120c.—Pearse, 1953:237.—Menzies and Miller, 1954: 141, 153.—George and Strömberg, 1968:251, 253 [San Juan Island, Washington; infesting *U. pugettensis*].—Şadoğlu, 1969:197.—Schultz, 1969: 321; fig. 512.—Strömberg, 1971:2 [San Juan Islands; infesting *U. pugettensis*].—Kozloff, 1974:148.—Miller, 1975: 285, 286, 305; pl. 64, fig. 16.

Phyllodurus [sp.].—MacGinitie, 1937:1035.
"Isopods."—Kozloff, 1973:233.

Remarks.—*Phyllodurus abdominalis* is known from only a moderate distance along the Pacific coast of North America, from southern British Columbia to central California, and it evidently infests only a single host species, *Upogebia pugettensis*. Nonetheless, it is very common in parts of its range, particularly the San Juan Islands and Tomales Bay, and it has been collected many times. It has been well described and illustrated, especially by Richardson (1905), so nothing need be added to its description here.

Status of *Phyllodurus robustus* Pearse, 1953

Pearse (1953) described a parasite of *Upogebia affinis* (Say) from Alligator Harbor, Florida (Gulf of Mexico) under the name of *Phyllodurus robustus*. In order to determine its status, I have examined the type-specimens of *P. robustus*, USNM 93719, of *Pseudione upogebiae* Hay, USNM 48369 and USNM 48370 (infesting *Upogebia affinis* at Beaufort, North Carolina) and of *Pseudione furcata* Richardson, USNM 29093 (infesting an unknown host off the coast of Virginia).

The original description of *Phyllodurus robustus* by Pearse (1953) was not adequate for one to ascertain the true nature of that species except that its assignment to the genus *Phyllodurus* was clearly erroneous. The type-specimens were mounted on a microscope slide and crushed and dissolved almost beyond recognition. Careful examination of them reveals most of the characters diagnostic for *Pseudione upogebiae*, other characters being indiscernible. Specifically, the female's pereopods bear prominent basal carinae, and its pleopods are deeply dentate, while the male has a distinctive outline, and its head is very reduced and fused with the first pereomere.

The reasons for Pearse's assignment of this species to the genus *Phyllodurus* are unclear. *Phyllodurus abdominalis*, as implied by its name, is an abdominal parasite, though Pearse (1953) clearly mentions that *P. robustus* infested its host branchially. To be sure, the host of *P. abdominalis* is *Upogebia pugettensis*, a congener of the host of *P. robustus*, *U. affinis*. This, however, is not in itself an adequate explanation, because Pearse (1945, 1947) twice recorded collecting *Pseudione upogebiae* infesting *Upogebia affinis* before he described *Phyllodurus robustus*.

Hay (1917) considered *Pseudione upogebiae* to be closely similar to *P. furcata*. Having examined the types and other specimens of *P. furcata*, I am satisfied that there is no question about the distinctness of *P. upogebiae* from *P. furcata*, even though they both infest the same host species, *Upogebia affinis*, at the same localities. The male of *P. furcata* remains undescribed, but specimens of it which I have seen are also clearly distinguishable from that of *P. upogebiae*.

Lemos de Castro (1965) speculated that *Phyllodurus robustus* might be a synonym of *Pseudione upogebiae*. He was of course unable to confirm that without examining the types of *Phyllodurus robustus* because of the inadequacy of the published description. His report of *Pseudione upogebiae* from Brazil makes this one of the most widespread of all western Atlantic bopyrids.

Synonymizing *Phyllodurus robustus* with *Pseudione upogebiae* makes the genus *Phyllodurus* once again monotypic, as is the new subfamily containing it, Phyllodurinae.

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